

# Ecological Correlates to Social Structure in Two Lemur Species in Madagascar

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**KEY WORDS** *Eulemur fulvus rufus*, *Eulemur rubriventer*, Group size, Patch use, Seasonality, Infant development

**ABSTRACT** In this study, I tested two hypotheses regarding the relationship of ecological variables (size, density, and distribution of patches) and infant developmental patterns to lemur social structure using two prosimian primates in Ranomafana, Madagascar: the rufous lemur (*Eulemur fulvus rufus*) and the red-bellied lemur (*Eulemur rubriventer*). Three predictions regarding the general effects of patch size and subgroup size on lemur feeding rates were supported: (1) Rufous lemurs used large patches; red-bellied lemurs used smaller patches; (2) larger subgroups of rufous lemurs used larger patches; and (3) rufous lemur feeding rates decreased significantly with increases in subgroup size and patch size, whereas size and patch size had no significant effect on red-bellied lemur feeding rates. However, food item size (fruit) had a more significant effect on rufous and red-bellied lemur feeding rates than either patch size or subgroup size. When similar-sized fruits were compared, rufous lemur feeding rates on small fruit were most affected by patch size, yet feeding rates on medium-sized fruit were most affected by subgroup size. Neither lemur species used patches in consistent ways seasonally. During periods of food abundance, rufous lemurs used many small, common, and clumped patches. In food scarcity periods, they used fewer, larger, rarer, and less clumped patches; groups migrated when food became most scarce. Red-bellied lemurs also used patches in variable ways, but these patterns were not linked with food availability. Finally, infant development patterns differed between lemur species; red-bellied lemur males cared for offspring and infants reached developmental landmarks faster than rufous lemur infants. Therefore, red-bellied lemur group size may be constrained by the need for additional infant care by other group members. In contrast, rufous lemur group size may be constrained by patch availability during the most critical period of food scarcity. © 1996 Wiley-Liss, Inc.

Two factors that are considered to significantly influence primate social structure (or group size) are ecological variables relating to the type of resources primates use and primate life history patterns. Some primatologists argue that primate group size is determined by the size, density, and distribution of food patches (Altmann, 1974; Wrangham, 1980; Leighton and Leighton, 1982; Wright, 1985, 1986; Terborgh, 1986; Terborgh and Janson, 1986; Janson and van

Schaik, 1988; Symington, 1988; Rodman, 1988; White and Wrangham, 1988; Strier, 1989; Chapman, 1990; Isbell, 1990; Janson, 1992). Others argue that primate social structure is constrained by life-history vari-

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ables, specifically infant development patterns and reproductive seasonality (Leutenegger, 1973; Wright, 1984; van Schaik, 1989; DeRousseau, 1990; Janson, 1992).

However, the majority of the ecological and life-history studies listed above used New World primates primarily as a model, although comparable data is available on Old World primates (Whitten, 1988) and apes (Gittens and Raemaekers, 1980; Leighton, 1987; Rodman, 1988; White and Wrangham, 1988). How well either of these explanations apply to Madagascar prosimians living in cohesive groups has yet to be determined, particularly since they have dramatically different life history patterns compared to anthropoids. Some of these unique life-history features include a highly seasonal reproductive system that is photo-periodically cued (Rasmussen, 1985), short gestation lengths, extreme energy costs during prenatal and postnatal states (Young et al., 1990), and lower basal metabolic rates (Richard and Nicoll, 1987; Young et al., 1990; Richard and Dewar, 1991).

In addition, in most ecological studies, primate species were compared that differed on the family or generic level, varied in body weight, or were found in different study sites. To avoid these problems, I will use data collected on sympatric populations of rufous lemurs (*Eulemur fulvus rufus*) and red-bellied lemurs (*Eulemur rubriventer*) to evaluate the ecological and life-history explanations for primate group size. Both lemur species are highly frugivorous, feed on many of the same plant species, and have low dietary diversity (Overdorff, 1993a). Despite these similarities, these two species maintain different group sizes. Rufous lemurs are found in multimale and multifemale groups (mean size = 8 individuals,  $n = 8$ ) and red-bellied lemurs live in small monogamous groups (mean size = 3 individuals,  $n = 12$ ). The general assumptions that underlie the ecological and life-history explanations for primate group size will be outlined below, and predictions are made regarding the relationship of feeding ecology and infant development patterns to red-bellied and rufous lemur group size.

Primatologists who argue that patch-use patterns determine primate group size make

two assumptions about how patches influence individual food intake that will, in turn, limit group size. The first assumption is that small patches are more rapidly depleted because they contain less food than large patches; therefore individual food intake should be correlated with patch size (Janson, 1988; Chapman, 1990). By this argument, animals that rely on food from small patches should have small group sizes so that group members can meet daily nutrient requirements. Conversely, animals that rely on food occurring in larger patches should be able to feed in larger subgroups and form larger permanent groups. For example, Wright (1986) found that family groups of night monkeys (*Aotus trivirgatus*) and titi monkeys (*Callicebus moloch*) used smaller patches than larger groups of squirrel monkeys (*Saimiri sciureus*). In addition, larger groups can be maintained as long as each individual is able to meet daily nutrient requirements and foraging effort does not exceed food intake (Janson, 1988).

The second assumption, which builds on the first, is that the number of individuals feeding at one time in a patch also will influence individual food intake (Wrangham, 1980; van Schaik et al., 1983; van Schaik and Noordwijk, 1986; Janson, 1988; Janson and van Schaik, 1988). In many primate species, foraging effort increases with increasing group size and an individual's food intake correspondingly decreases (Clutton-Brock and Harvey, 1977; Waser, 1977; Janson, 1988). For example, Chapman (1990) found that individuals in smaller groups or subgroups of howling monkeys and spider monkeys (see also Strier, 1989) ate more food in patches and traveled less than individuals in larger groups or subgroups. Therefore, given these two assumptions, patch size and subgroup size will both be important variables that constrain primate feeding rates and, ultimately, influence group size.

If patch size is correlated with group size and influences food intake, I expect that rufous lemurs will use significantly larger patches than red-bellied lemurs because they live in larger groups (Hypothesis I, Prediction 1a). In addition, if increasing subgroup size affects food intake, larger subgroups of rufous lemurs should have lower

feeding rates than smaller subgroups. Therefore, larger subgroups should use larger patches to compensate. In contrast, because red-bellied lemur groups contain only two or three adult-sized animals, patch size and subgroup size should not have a strong effect on food intake in this species (Prediction 1b). It also is assumed that the difference in group size between red-bellied and rufous lemurs is large enough to promote ecological differences.

The density and distribution of patches are additional ecological variables that can influence group size. These two variables can affect the distance and the amount of time an individual spends traveling between patches. Animals that rely on high-density patches will travel less and will travel shorter distances between patches than animals relying on low-density patches. Patch distribution also affects travel time and distance in similar ways. If patches are widely scattered, animals must travel further. In contrast, travel time may be reduced if patches are more uniformly distributed. Because travel time is costly, animals should feed in patches that maximize food intake (or food quality) and minimize travel costs (Chapman, 1988; Symington, 1988). Therefore, it is expected that small groups, such as red-bellied lemur groups, will use patches that large groups avoid (low-density or widely distributed) because they incur higher energetic costs. Large groups, such as rufous lemur groups, will exploit patches that are less costly (high density and uniformly distributed; Prediction 2).

Finally, how primate groups use patches seasonally has not been widely considered (but see Whitten, 1988; Chapman, 1988; Symington, 1988; Chapman et al., 1994). If patch choice consistently influences group size, one of three patterns should be observed: (1) patch-use patterns should remain constant throughout the year, (2) groups should remain cohesive but should form different subgroup sizes to adjust to the different types of patches available, or (3) groups should fragment to accommodate changes in patch availability, which is typical of most fission–fusion species (Chapman, 1988; Symington, 1988; White and Wrangham, 1988; Strier, 1990). Because neither lemur

species is known to exhibit a fission–fusion social structure, it is expected that patch-use patterns should be consistent for red-bellied and rufous lemurs across seasons (Prediction 3a) or that rufous lemurs should adjust subgroup size to patch availability while remaining cohesive (Prediction 3b).

Ecological factors alone may not always be sufficient to determine the variation seen in primate group size. Researchers have found that life-history patterns also can affect primate group size (Leutenegger, 1973; Wright, 1984; van Schaik, 1989; DeRousseau, 1990; Janson, 1992; Pereira, 1993; van Schaik and Kappeler, 1993). These authors suggest that in some primates, life-history patterns such as infant development rates, infant care, and reproductive seasonality may have a greater role in determining group size than previously thought. The need for infant care of precocial, fast-growing, heavy infants (relative to maternal body weight) appears to constrain group size in small-bodied monogamous and polyandrous primates (Fragaszy et al., 1982; Wright, 1984, 1990; Goldizen, 1987a,b, 1989). The main assumption these authors make is that paternal certainty is assured by living in a small group, which makes paternal care more likely to occur. On the basis of this theory, it is expected that red-bellied lemur infants should grow faster and reach developmental landmarks faster than rufous lemur infants (Hypothesis II, Prediction 1). If infants do grow faster, other group members (fathers and juveniles) also may assist with the care of red-bellied lemur offspring.

## MATERIALS AND METHODS

### Study site

The study site was located in the Ranomafana National Park (RNP) region, a large (40,000 ha), southeastern stretch of rain forest in Madagascar between 47° 6' and 47° 42' E longitude and 21° 0' and 21° 24' S latitude, which ranges from montane cloud forest (1,500 m) to lowland rain forest (500 m). The site for this study, Vatoharanana, was approximately 5 km south from the Duke University Research station at Ranomafana. Vatoharanana is a high montane rain forest (altitude: 1,125 m) with an annual rainfall

of 2,300 mm during this study. The site currently has a 3.5 km<sup>2</sup> trail system. Ten sympatric species of prosimian primate are found in the area in addition to the two study species.

### Methodology and statistics

**Patch size, food intake, and subgroup size (Prediction 1a, 1b).** Two groups of red-bellied lemurs (RB, group size =  $\bar{x}3$ ) and one group of rufous lemurs (RL, group size =  $\bar{x}9$ ) were followed from dawn to dusk 5–8 days a month from July 1988 through August 1989 with the help of a field assistant. A second group of rufous lemurs (group size =  $\bar{x}7$ ) and a third group of red-bellied lemurs (group size =  $\bar{x}3$ ) were observed throughout the study on an opportunistic basis. Over 3,000 hr of data were collected, and data are presented from August 1988 through August 1989. Data, however, are unavailable on rufous lemurs for April 1989 because they migrated from the study site. Differences were tested between study groups within each species using a Mann–Whitney *U* test, and results were combined if no differences were found.

A combination of focal-animal and all-occurrence sampling was used to quantify feeding behavior (Altmann J, 1974). I measured patch size, subgroup size, and the amount of food removed from the patch by the focal animal to test predictions regarding patch size and its influence on an individual's food intake. To accomplish this, an adult male and female focal animal were each followed by one observer exclusively on each sampling day. Focal samples were balanced between all adult individuals in each study group. Individuals were marked with colored collars and pendants or radio collars.

As the focal animal was followed, all feeding bouts (>15 sec) were recorded. Observers recorded five types of data each time the focal animal began feeding: feeding bout duration, patch size, number of individuals feeding with the focal animal (subgroup size), number and type of food removed by the focal animal, and location of the patch (if greater than 5 cm DBH). The word "patch" is defined here as a single tree or liana used by a lemur for food and includes fruit, flower, and leaf sources. Patch size was calculated

for every tree over 5 cm DBH used by the focal animal. Crown volume, which is considered a good estimate of food availability, was used as the measurement of patch size (Janson, 1988). Volume was calculated by visually estimating crown radius (m), crown depth (m), crown shape (circular, cylindrical, triangular, dome), and measuring diameter at breast height (DBH). When animals fed on liana species, the area of the tree crown in which the liana was growing was considered as the patch size. The area covered by the liana was estimated if lianas were hanging between trees.

The total number of individuals feeding at one time in a patch (including the focal animal) was defined as a subgroup, and subgroup size was counted at the beginning and end of the bout and at 2 min intervals during each feeding bout. A mean subgroup size was determined for each feeding bout by averaging the total number of subgroup counts for that bout.

Individual food intake was quantified by counting the number of fruits eaten per feeding bout by each focal animal. To control for the variation in bout length, the feeding rate for each bout was calculated by dividing the total number of fruits eaten during each bout by the length of the feeding bout. Because most of the food counts collected were on fruits (92%), only feeding rates for fruits are used in this analysis. Because both lemur species are highly frugivorous, fruit feeding rates probably represent their patch-use patterns adequately.

One problem with previous studies is that the size and weight of the food item being eaten is rarely considered as a variable that may influence feeding rates in addition to patch size and subgroup size. In this study, 20 samples of ripe and unripe fruit from each plant species eaten by either lemur species were measured (length and width). Only a small sample of fruits were weighed during this study due to a malfunctioning balance scale; it is assumed here that fruit size will be roughly correlated with fruit weight (Overdorff and Strait, unpublished data). The mean fruit length (rounded to the nearest whole number) was calculated for each plant species and a frequency distribution was constructed for the number of fruit spe-

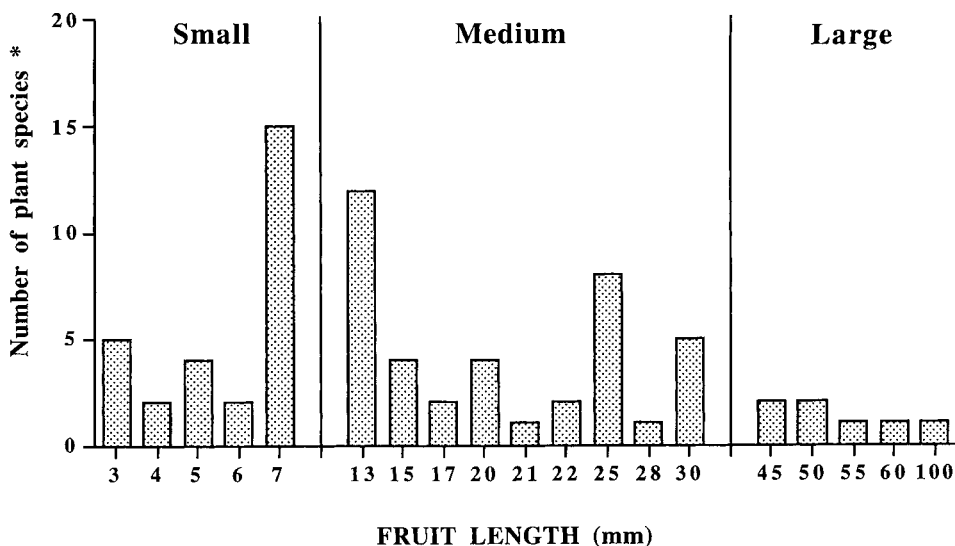


Fig. 1. Frequency distribution of fruit length for all species of fruit eaten by rufous and red-bellied lemurs during the study period. All size classes (rounded to the nearest whole number) are represented. Gaps exist in fruit length sizes because no fruits fell into that size category (e.g., no fruits were recorded that were 8–12

mm). Category names are listed above each section. The sizes of ripe and unripe fruit were considered separately so that unripe fruit of one species may be included in one category while ripe fruit (which is typically larger) may be included in another category.

cies for each fruit length (Fig. 1). Unripe fruit are often smaller than ripe fruit so that it is possible that the same species of plant could fall into two categories. Based on this distribution, fruits were categorized as small (3–7 mm), medium (13–30 mm), or large (>45 mm).

To test the patterns discussed in Prediction 1 (see introductory remarks), three statistical tests were conducted. First, a Mann-Whitney *U* test was used to compare differences in patch size and subgroup size between lemur species. In addition, a Spearman's coefficient of rank correlation was used to test the relationship between subgroup size and feeding rate within each lemur species. Finally, a multiple regression analysis was used to assess the relative influence of patch size, subgroup size, and fruit size on feeding rates for both lemur species (Statview II). Data were log transformed to improve linearity and analyzed in two ways. First, partial regressions were run for each lemur species by alternately holding subgroup size, patch size, and fruit size constant using feeding rate as the dependent variable. Second, the relative influence of patch size

and subgroup size on feeding rates was examined further by comparing fruits of similar size using the predetermined size categories.

#### **Patch density and distribution (Prediction 2).**

**Relative density.** Botanical samples were used to determine patch density of plant species used by the lemurs. Ten botanical plots were placed randomly in 10 areas of the study site (two 25 × 25 m plots, and eight 50 × 5 m plots; total area = 0.33 ha). Each tree and liana over 2.5 cm diameter at breast height was identified and measured using techniques previously established (Gentry, 1982). Plant species were listed in order of density (total number of each plant species as represented in all plots) and divided into quartiles so that each plant species could be categorized as common, moderately common, moderately rare, and rare. The first two quartiles were considered to represent relatively common plant species. The percentage of time each lemur species spent feeding on common and rare plant species then was calculated daily.

**Distribution.** The botanical plots described in the previous section measure the relative density of plant species used by these two lemur species, but do not indicate the distribution of patches actually used. One method often used by other researchers to determine patch distribution is the distance traveled between patches. In this instance, it is assumed that long distances indicate clumped patches while shorter distances indicate uniform patches (see Terborgh, 1983; Wright, 1986; Garber, 1988). There are two limitations, however, to using the distance traveled between patches as a measure of patch distribution. First, relative patch density may be a confounding variable because rare patches may be more widely spaced in the habitat than common ones. Another limitation is that by only calculating the distance traveled between patches, the actual placement of patches in the habitat is not considered. For example, patches may be uniformly distributed but widely spaced so that interpatch distance is long.

Therefore, to look at patch placement, each new patch used by either lemur species was labeled with a numbered tree tag so that subsequent visits to the same patch could be recorded. All patches used by each lemur group daily were plotted onto the home range map. The home range of each study group was divided into 0.25 ha quadrants. Only quadrants through which each daily path length passed were considered. The number of quadrants containing zero, one, two, three, four, or five patches (no quadrant contained more than five patches) was calculated for each lemur species for every day of observation. Using these data, a daily coefficient of dispersion (CD) was determined for each study group:

$$CD = s^2/Y$$

where  $s$  equals the standard deviation and  $Y$  is the arithmetic mean of the number of trees per 0.25 ha quadrant per day. If  $CD = 1$  it was assumed that patch distribution was random, if  $CD < 1$  the distribution was uniform, and if  $CD > 1$  the distribution was clumped (Sokal and Rolf, 1981).

The Mann-Whitney  $U$  test was used to test for differences between lemur species

for number of patches used, percentage of time spent feeding on common vs. rare plant species, and daily coefficients of dispersion. Data were not averaged or lumped for these overall comparisons.

### **Consistency and seasonality in patch use (Prediction 3).**

**Consistency.** A Kruskal-Wallis one-way analysis of variance was used to examine consistency in patch use within lemur species. The following ecological variables were grouped into semimonthly intervals that corresponded to phenological sampling periods: (1) patch size, (2) percentage of time spent feeding on common and rare patches, (3) subgroup size, (4) coefficient of dispersion, and (5) number of patches used.

**Seasonality.** In July 1988, a sample of 104 trees, representing four mature trees each of 26 plant species, were selected that were known to have fruits, flowers, or leaves consumed by primates at RNP. All trees in the sample were checked for the presence of fruit, flowers, and new leaves twice a month (on the 15 and 30) throughout the study and until June 15, 1990. The abundance of fruit, flowers, and new leaves was measured by ranking each phase on a scale from 0 (not present) to 5 (full fruit, flowers, and/or new leaves). This ranking scale was called an amplitude score and reflected the proportion of the tree's crown containing a particular phenological phase. Food availability was determined using the following formula:

$$FA = \sum_{i=0}^i CV^* (A/5)$$

where  $FA$  = food availability,  $i$  = number of trees with fruit, flowers, and/or new leaves in each sample,  $CV$  = crown volume, and  $A$  = amplitude score. The amplitude score is divided by five (based on the 0–5 ranking scale) to give an estimate of the proportion of the crown volume actually containing fruit, flowers, or new leaves).

Because the phenological data were ordinal and nonlinear, the relationship between semimonthly food availability and patch use was tested using Spearman's rank correlation coefficient (Sokal and Rolf, 1981). Ecological data for each species were averaged

into semimonthly intervals that coincided with phenological samples. These data included: (1) patch size, (2) percentage of time spent feeding on common and rare patches, (3) subgroup size, (4) number of patches eaten in, and (5) coefficient of dispersion.

**Infant development.** Ad libitum notes were collected on unusual or infrequent behaviors, specifically, male care and infant developmental landmarks in both lemur species. Male care was defined as an adult male holding or carrying the infant while other group members traveled, rested, or fed. The beginning and end time of each male care bout was noted. Developmental landmarks were determined prior to the study and included the first time the infant climbed off the mother, fed on solid food, played with others, traveled independently, the first time the mother rejected the infant from being carried and from the nipple, and when males first carried infants. The age of the infant (in days) was noted when each infant reached a developmental landmark, and was compared between groups and species for differences.

## RESULTS

### Hypothesis 1, Prediction 1

**Patch size.** Rufous lemurs used slightly larger patches (RL: mean = 478.64 m<sup>3</sup>, SE = 27.02,  $n = 1,400$ ) overall than red-bellied lemurs (RB: mean = 421.94 m<sup>3</sup>, SE = 22.39,  $n = 2,002$ ; Mann-Whitney  $U$  test:  $Z = 2.76$ ,  $df = 1$ ,  $P < 0.006$ ). However, the patch sizes used by each lemur species varied dramatically and some of the largest patches observed were used by red-bellied lemurs (RL: range 0.13–6,240 m<sup>3</sup>; RB: range 0.13–6,280 m<sup>3</sup>).

**Subgroup size.** An entire group of rufous lemurs rarely fed simultaneously in the same patch, and subgroups were larger than red-bellied lemur groups (Mann-Whitney  $U$  test:  $Z = 3.11$ ,  $df = 1$ ,  $P < 0.002$ ). Subgroups of three and five rufous lemurs were observed most frequently, and larger patches accommodated larger subgroups ( $r_s = 0.53$ ,  $P < 0.0001$ ,  $n = 1,400$ ). Larger subgroups, however, experienced lower feeding rates ( $r_s = -0.31$ ,  $P < 0.0001$ ,  $n = 326$ , Fig. 2A).

Excluded group members either waited to feed in the next patch visited, took turns with other members feeding, or waited until the members of the initial subgroup stopped feeding. In contrast, red-bellied lemur groups rarely fed apart. Consequently, subgroups did not fluctuate with patch size ( $r_s = 0.03$ , NS,  $n = 2,002$ ) or significantly influence feeding rates ( $r_s = 0.04$ , NS,  $n = 170$ ; Fig. 2B).

**Relationship of patch size, subgroup, fruit size, and feeding rate.** Fruit size was the best predictor of feeding rate for both lemur species when all patches were considered (Figs. 3, 4). Feeding rate decreased with increasing fruit size in both lemur species; subgroup size also strongly affected feeding rates in rufous lemurs (Fig. 3). When comparable-sized fruits were compared, different patterns emerged. Patch size influenced feeding rates when rufous lemurs ate small fruits (3–7 mm). In contrast, subgroup size significantly influenced feeding rates when rufous lemurs ate medium-sized fruits (13–30 mm; Fig. 5). Neither variable influenced feeding rates on large fruits, and larger fruits were found in larger patch sizes ( $r_s = 0.38$ ,  $P < 0.0001$ ,  $n = 2,600$ ). In addition, subgroup size or patch size did not affect red-bellied lemur feeding rates when fruits of similar sizes were compared (small fruits  $F$  test = 1.21, NS; medium fruits  $F$  test = 1.60, NS; large fruits  $F$  test = 0.90, NS).

### Prediction 2: Patch density and distribution

**Patch density.** There was no difference in the amount of time either lemur species spent feeding on common or rare plants (Mann-Whitney  $U$  test  $Z = 0.13$ ,  $df = 1$ , NS). Both species spent time feeding in common patches more often on a daily basis (RL: mean = 58.56%, SE = 3.24,  $n = 111$  days; RB: mean = 58.78%, SE = 3.16,  $n = 83$  days).

**Patch distribution.** When all patches were considered, rufous lemurs used patches that were highly clumped ( $CD = 8.13$ ) while red-bellied lemurs used patches that were randomly distributed ( $CD = 1.01$ ). This

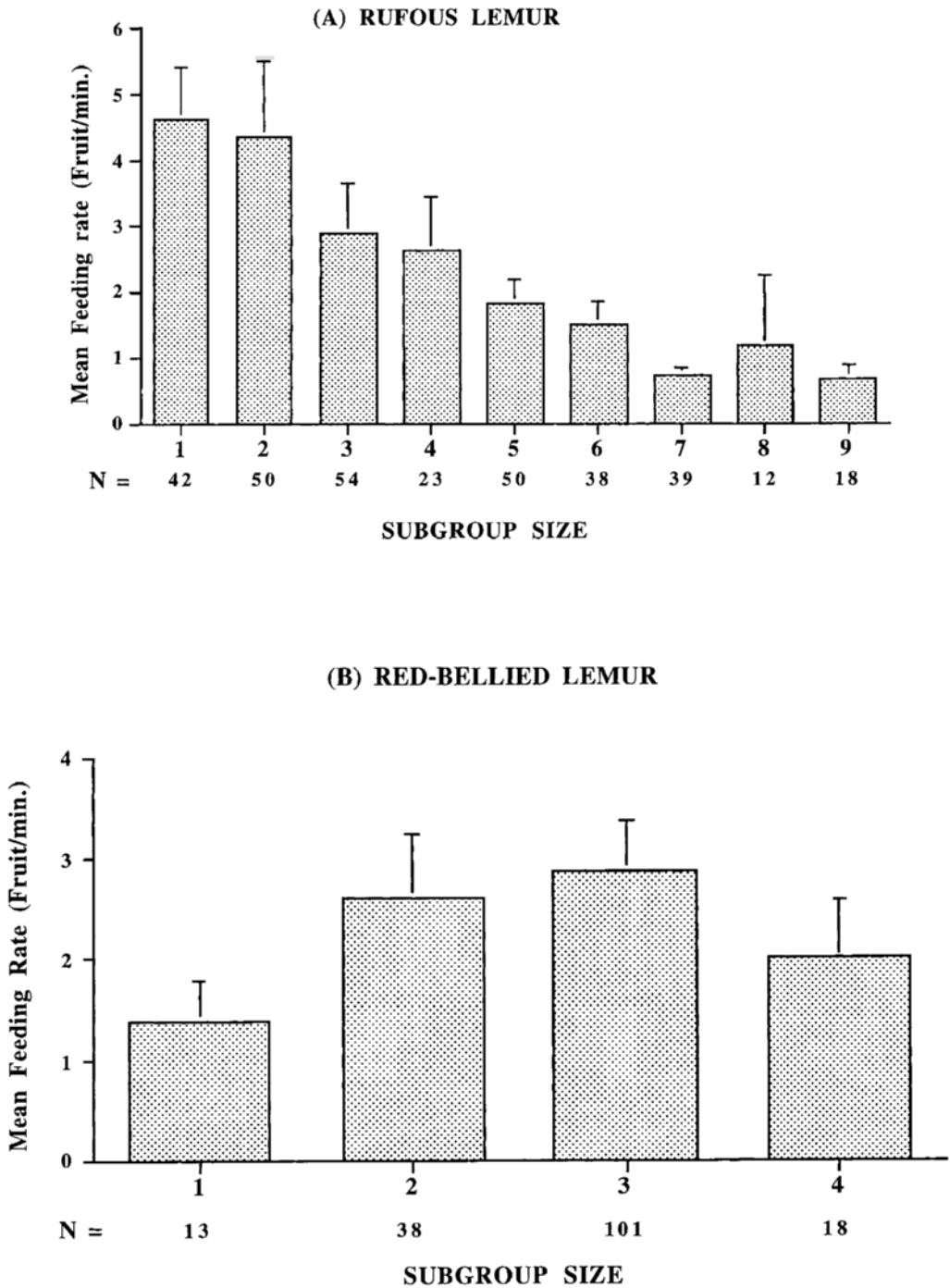


Fig. 2. The relationship of mean feeding rate (fruit/min.) and subgroup size for rufous lemurs (A) and red-bellied lemurs (B). Bars represent standard errors, and sample sizes for each subgroup size are listed below each bar.



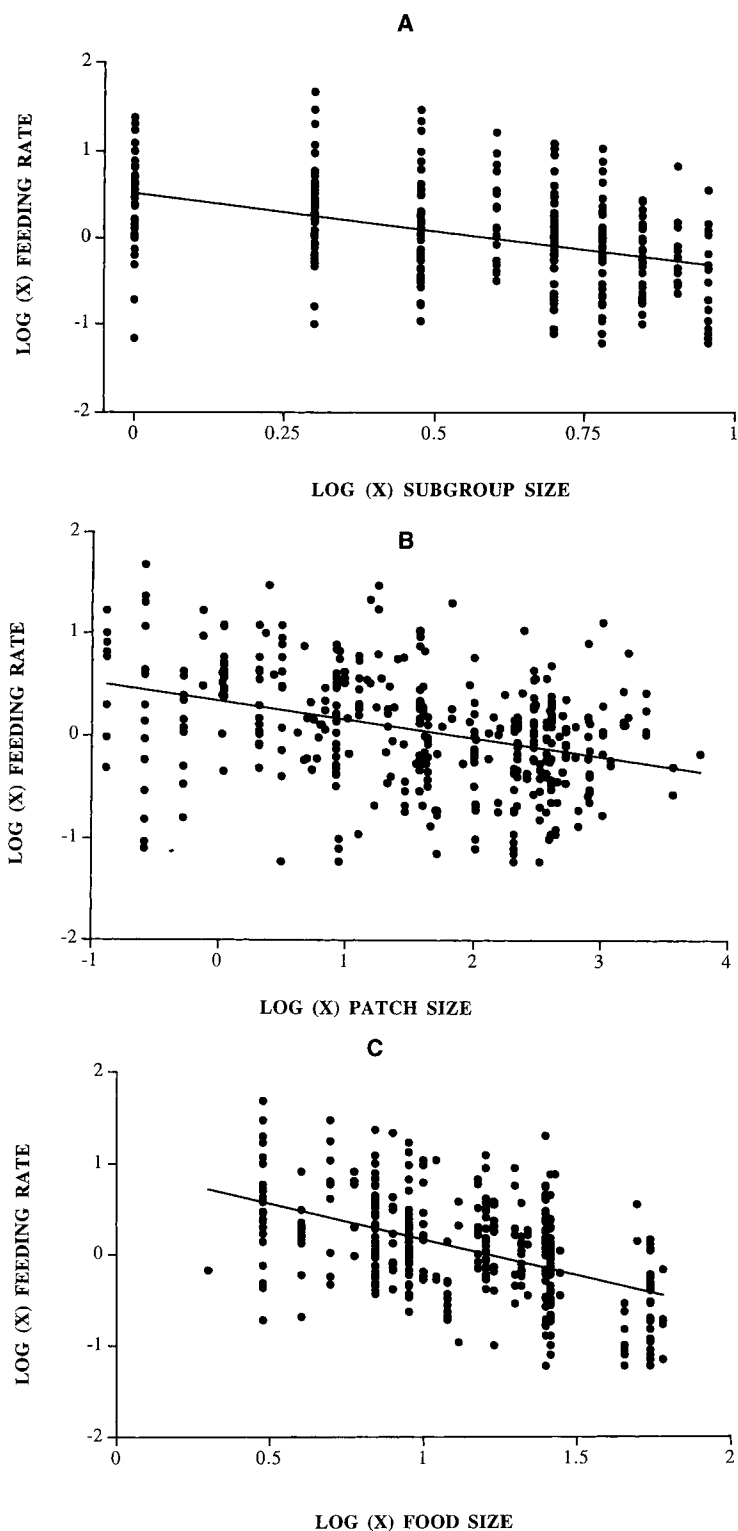


Fig. 3. Multiple regression analysis examining the effects of subgroup size, patch size, and food size on feeding rate for rufous lemurs ( $F$  test = 67.99,  $P < 0.0001$ ). **A** demonstrates the effect of subgroup size on feeding rate by holding patch size and food size constant (partial  $F$  = 18.13,  $P < 0.0001$ ), **B** demonstrates

the effect of patch size on feeding rate by holding subgroup size and food size constant (partial  $F$  = 5.80,  $P < 0.02$ ), and **C** demonstrates the effect of food size on feeding rate by holding patch size and subgroup size constant (partial  $F$  = 108.59,  $P < 0.0001$ ).

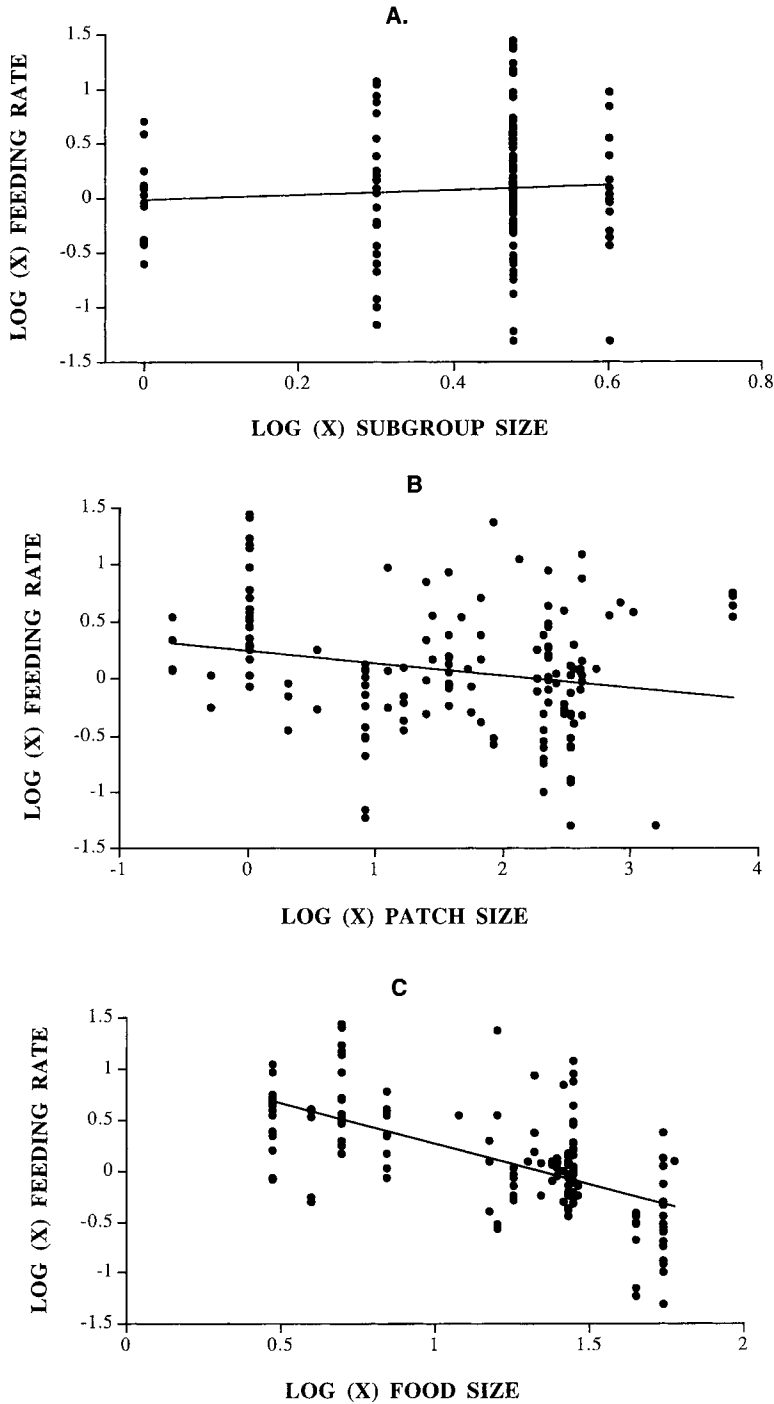


Fig. 4. Multiple regression analysis examining the effects of subgroup size, patch size, and food size on feeding rate for red-bellied lemurs ( $F$  test = 34.32,  $P < 0.0001$ ). **A** demonstrates the effects of subgroup size on feeding rate holding patch size and food size constant (partial  $F$  = 0.39, NS), **B** demonstrates the effects of

patch size on feeding rate by holding subgroup size and food size constant (partial  $F$  = 0.70, NS), and **C** demonstrates the effect of food size on feeding rate by holding patch size and subgroup size constant (partial  $F$  = 89.43,  $P < 0.0001$ ).

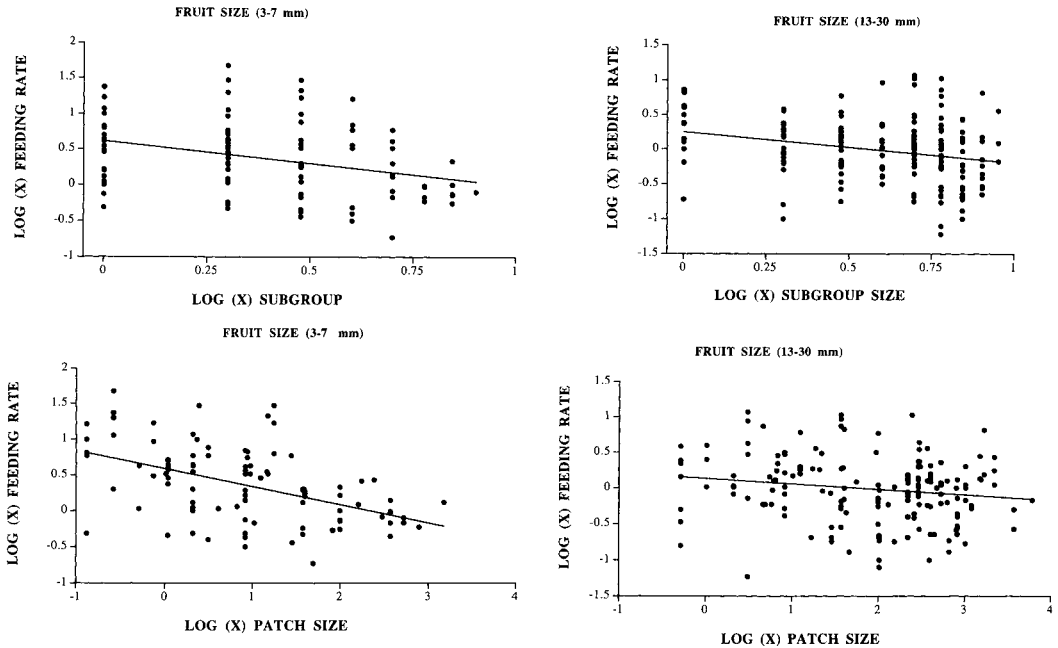


Fig. 5. Multiple regression analyses for small fruits ( $F$  test = 18.65,  $P < 0.0001$ ) and medium fruits ( $F$  test = 8.17,  $P < 0.0001$ ) eaten by rufous lemurs. Patch size was a better predictor of feeding rate on small fruits than subgroup size (patch size partial  $F$  = 19.86,  $P < 0.0001$ ; subgroup size partial  $F$  = 1.99, NS). For me-

dium fruits, subgroup size was a better predictor of feeding rate than patch size (patch size partial  $F$  = 1.5, NS; subgroup size partial  $F$  = 11.06,  $P < 0.001$ ). Feeding rates on large fruits were unaffected by either variable ( $F$  test = 0.93, NS).

trend was also apparent on a daily basis. The mean CD for rufous lemurs was higher (mean = 1.87, SE = 0.34) than that for red-bellied lemurs (mean = 1.03, SE = 0.31; Mann-Whitney  $U$  test  $Z$  = 4.27,  $P < 0.0005$ ).

### Prediction 3: Consistency and seasonality of patch-use patterns

**Seasonal patterns.** Seasonal fruiting, new leafing, and flowering patterns were observed during the study and subsequent months after behavioral observations were complete. Fruit was most available from August 1988 through February 1989, and was most scarce between April and August 1989. The second fruit availability peak in the second half of August 1989 was not as high and was much shorter than the previous year's pattern. A much higher fruit peak (compared to previous years) was observed between April and June 1990 (Fig. 6A).

Flower and new leaf availability also showed similar variability in peak times and

amplitude. Four distinct peaks in flower availability occurred in August 1988, November 1988–January 1989, September–October 1989, and February–March 1990 (Fig. 6B). New leaf availability peaked between November 1988 and January 1989, and again in March and April 1989, but the largest peaks observed occurred in November and February 1990 (Fig. 6C).

**Consistency.** Neither lemur species demonstrated consistent patch-use patterns throughout the study (Table 1). Both lemur species significantly varied in the size of patches used, subgroup size, amount of time spent feeding on common species across semimonthly periods (relative plant density), coefficient of dispersion (only rufous lemurs varied significantly), and number of patches used.

The only consistent seasonal similarity observed was that both lemur species used large patches when fruit was most scarce (Table 2). Red-bellied lemurs also used

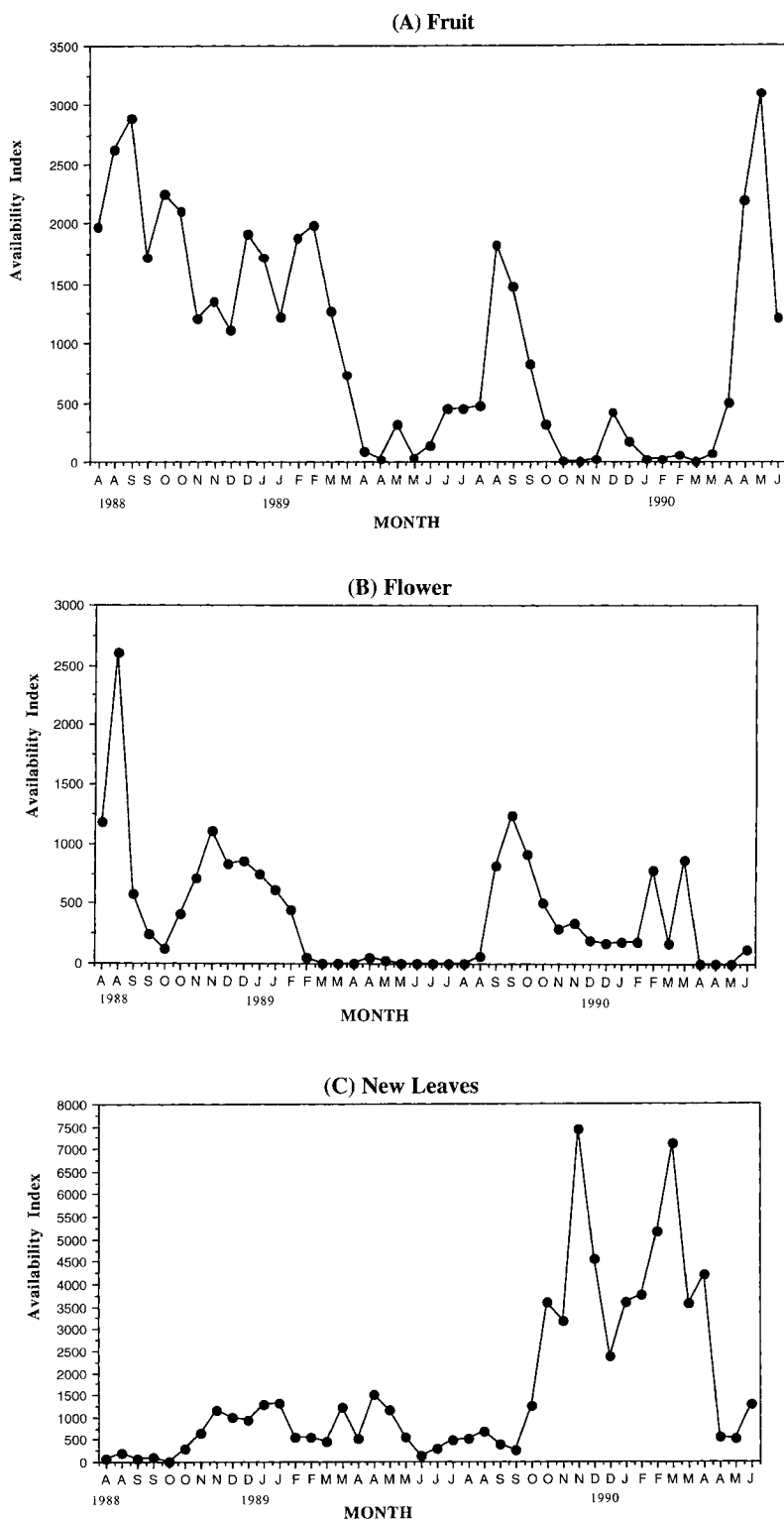


Fig. 6. Food availability index for (A) fruit, (B) flowers, and (C) new leaves from August 1988 through June 1990. Semimonthly intervals from August 1988 through August 1989 correspond to behavioral sampling.

TABLE 1. Test for variability in patch-use patterns throughout the study for rufous lemurs and red-bellied lemurs using the Kruskal-Wallis one-way analysis of variance test<sup>1</sup>

Ecological variables	Rufous lemur (d.f. = 23) <sup>2</sup>	Red-bellied lemur (d.f. = 25)
Patch size (m <sup>2</sup> )	214.80***	189.42***
Subgroup size	51.20***	43.23***
Relative plant density	53.81***	64.35***
Number of patches used daily	54.70***	25.40**
Coefficient of dispersion	35.54***	1.90

<sup>1</sup> Data were grouped by semimonthly periods that corresponded to phenological sampling. H values are listed in each cell, \*\* $P < 0.001$ , \*\*\* $P < 0.0001$ .

<sup>2</sup> Degrees of freedom are fewer for rufous lemurs as they migrated in April from the site.

larger patches more often when new leaves were scarce. In contrast, all of the variables examined for rufous lemurs were correlated with changes in fruit availability. When fruit was available, rufous lemurs fed in smaller subgroups that used more, small, common patches that were clumped. During scarcity periods, they fed in larger subgroups that used fewer, larger, and rarer patches that were more uniform in distribution. Across semimonthly periods, rufous lemurs continued to use patches that were clumped ( $CD > 1.0$ ), but they tended to use less clumped patches when fruit was scarce. Red-bellied lemur CDs remained close to 1.0 in each semimonthly period.

#### Life history patterns: Infant development

The two differences observed in infant development patterns between lemur species were the degree of male care and the timing of infant developmental landmarks. First, red-bellied lemur males assisted in the care of offspring while rufous lemur males did not. Male care commenced when infants were 20 days old in Group II and 32 days old in Group I. Male red-bellied lemurs held infants for 5–12 min at a time while the adult female fed or rested (mean = 7.4 min.,  $SD = 3.45$ ,  $n = 25$ ). Males also carried infants for 15–55 min when the group traveled (mean = 39.6 min.,  $SD = 22.2$ ,  $n = 22$ ). The number of times males carried infants also varied slightly, but not significantly between groups (Group I  $n = 17$ ; Group II  $n = 30$ ,  $G = 3.64$ , d.f. = 1, NS); juveniles never held or carried infants. Once infants reached 55

days of age, the adult female refused to carry the infant and the infant either traveled independently or was carried by the adult male. Male care was not observed after infants reached 100 days of age. Red-bellied lemur infants also reached developmental landmarks more quickly than rufous lemur infants (Table 3). In all cases, red-bellied lemur infants reached developmental landmarks sooner than rufous lemurs. Rufous lemur infants consistently engaged in novel behavior 2 weeks later than red-bellied lemur infants.

#### DISCUSSION

In this study, some of the predictions made concerning individual ecological correlates to group size were supported. However, the relationship of patch size, subgroup size, fruit size, and feeding rates to primate group size is a complex one. Patch-use patterns were not consistent within species or across seasons, and lemur species did not follow all predicted patterns.

In this study, many of the predicted relationships for rufous lemurs and red-bellied lemurs were supported when individual ecological variables such as patch size and subgroup size were considered in relation to feeding rates. For example, rufous lemurs used slightly larger patches than red-bellied lemurs (Prediction 1a). Rufous lemur feeding rates also decreased significantly with an increase in subgroup size, and larger subgroups of rufous lemurs tended to use larger patches. Finally, subgroup size and patch size had no significant effect on feeding rates in red-bellied lemur groups (Prediction 1b).

However, the relationship between patch size and subgroup size was more complex when fruit size was considered. Although rufous lemurs used larger patches than red-bellied lemurs, patch size was not a good predictor of either lemur species' feeding rates. In this study, feeding rates decreased with an increase in patch size. Raw counts of fruits consumed also demonstrated a similar trend (Overdorff, 1991). This differs from other researchers' observations that food intake usually increases with increasing patch size (Chapman, 1988; Janson, 1988; White and Wrangham, 1988). These studies, how-

TABLE 2. Spearman's rank correlation of ecological variables to seasonal changes in fruit (FR), flower (FL), and new leaf (NL) availability

Ecological variables	Species	Food availability		
		FR	FL	NL
Patch size (m <sup>3</sup> )	Rufous lemur	-0.44*	-0.23	-0.47
	Red-bellied	-0.63*	-0.26	-0.85**
Subgroup size	Rufous lemur	-0.59*	0.23	0.13
	Red-bellied	0.02	0.26	0.08
Relative plant density	Rufous lemur	0.73*	-0.47	0.41
	Red-bellied	0.38	-0.35	0.19
Number of patches used daily	Rufous lemur	0.67*	0.19	0.80**
	Red-bellied	0.22	0.54	0.09
Coefficient of dispersion	Rufous lemur	0.80*	0.01	0.72*
	Red-bellied	0.02	0.04	0.03

\*  $P < 0.03$ .\*\*  $P < 0.003$ .\*\*\*  $P < 0.001$ .TABLE 3. List of developmental landmarks compared between the infants of rufous lemurs and red-bellied lemurs<sup>1</sup>

Behavior	Rufous lemurs n = 3 <sup>2</sup>	Red-bellied lemurs n = 2 <sup>3</sup>
First off mother	26	10
Play with other group members	42	26
Locomote independently	55	42
Eat solid food	55	40
Rejected by mother (nipple)	96	110
Rejected by mother (riding)	56	30
Male care	Never observed	20/32 <sup>4</sup>

<sup>1</sup> The age of the infant in days when each of these behaviors was first observed is recorded. In all cases with the exception of male care, the age of the infants in each species was the same when they first engaged in each of these behaviors.

<sup>2</sup> Sample size includes an infant male in Group I who disappeared when he was 69 days old and two infants observed in Group II who both survived.

<sup>3</sup> Sample size includes an infant male from Group I who died at 7 months of age (post-weaning), and an infant female in Group II who survived.

<sup>4</sup> First age represents the female infant from Group II and the second age represents the infant male from Group I.

ever, did not take into account how food item size might influence feeding rates in addition to subgroup size and patch size. First, an individual could eat fewer fruits per bout if the fruits are large. Second, individual handling time of larger fruits most likely increases. Finally, plant species that produce larger fruits also occur in larger patches at this site. Together, these three factors could contribute to a decrease in feeding rate in larger patches. Although larger groups of rufous lemurs do not seem to benefit from larger-sized patches the way that other primates do (in that their feeding rates are lower), the size of the fruits being consumed

may be sufficient so that rufous lemurs can still maintain larger group sizes.

However, rufous lemur patch-use patterns become more complicated when similar-sized fruits were compared. Patch size or subgroup size was more influential on feeding rates depending on which size category of fruit was used. For example, feeding rates on small fruits declined with patch size (but not significantly with subgroup size). In contrast, feeding rates on medium-sized fruits declined with increasing subgroup size rather than patch size. No significant interaction between these variables was observed for large fruits.

The differences reported above as to whether patch size or subgroup size influence rufous lemur feeding rates may be the result of other confounding variables in addition to fruit size such as food preferences, quality, and the degree of ripeness (Whitten, 1988). In this study, rufous lemurs fed on more unripe fruits and mature leaves while red-bellied lemurs preferred ripe fruits (Overdorff, 1993a). It is possible that, like the brown lemur (*Eulemur fulvus fulvus*; Ganzhorn, 1988, 1989), rufous lemurs have a higher tolerance for secondary compounds found in unripe fruit and mature leaves. If so, the amount of food actually available in similar-sized patches would be different for the two lemur species. For example, if a patch is 300 m<sup>3</sup> but contains only 30 ripe fruit and 300 unripe fruit, the patch would be "large" and contain more food for rufous lemurs but be "small" and contain less food

for red-bellied lemurs. Therefore, larger patches with fewer ripe fruit could limit feeding rates. However, if the 30 ripe fruit were large (for example, *Canarium madagascariensis*, mean fruit length = 50 mm) so that a red-bellied lemur or a rufous lemur could eat one or two fruits and be satiated, the patch may be sufficiently "large" to support a group of rufous lemurs or red-bellied lemurs despite its physical size. Finally, if these 330 hypothetical fruit were small and distributed throughout a large-sized patch (*Harungana madagascariensis* fruits, for example, are approximately 3 mm in size and occur in large patches: 1,060–6,080 m<sup>3</sup>), rufous lemur feeding rates could be lower because larger subgroups tend to feed in larger-sized patches and could deplete the patch more quickly. Therefore individual feeding rates on smaller fruits in larger patches may be lower than small fruits in small patches.

Janson (1988) also has shown that not all patches are limiting based on size. Ripening time, synchrony, and predictability of food are other factors that may influence how much food is actually available to an individual. For example, a large patch producing a few fruit slowly over time could be a more limited food supply than a small patch that produces copious amounts of fruit in a short interval. In this study, many of the plant species that have medium-sized fruits (66.67%) produce fruits over a 2–4 month period or do not produce fruits predictably from season to season (Overdorff, 1991; Hemingway, 1995; see Fig. 6). Medium-sized fruits also are found in a wide range of patch sizes at this site (0.52–3,726.6 m<sup>3</sup>). Therefore, rufous lemur subgroup size may be a stronger influence on feeding rate than patch size for these kinds of fruits.

As a result, the flexibility demonstrated by both lemur species in size and types of patches used may be an adaptation to unpredictable and unseasonable phenological patterns. These phenological factors may place an upper limit on lemur group size, which is lower than most arboreal Old World and New World primates that use abundant, predictable food sources year round and/or rely on keystone patches seasonally that are abundant and predictable (Terborgh, 1985). This hypothesis needs to be tested further

by comparing variability in group size and longer-term phenological patterns at this site and others in Madagascar.

Furthermore, ecological patterns observed in other primate populations may not apply to Malagasy primates due to population differences. For example, red-bellied lemurs did not exclusively use small patches year round as has been observed in studies of other monogamous primates (*Aotus* and *Callicebus*, Wright, 1986; *Hylobates* sp., Leighton, 1987). In these studies, small groups were consistently excluded from large patches by large groups (Terborgh, 1983; Wright, 1986; Cheney, 1987; Waser, 1987). Accordingly, access to large patchy fruit sources in Manu National Park in Peru may be more contested because the density (300/km<sup>2</sup>), biomass, and average group size of primates is much higher (Terborgh, 1983) than in RNP (density 45/km<sup>2</sup>; Overdorff, 1991).

Contrary to Prediction 3a, rufous and red-bellied lemurs used patches in inconsistent ways throughout the study. However, some patch-use strategies seemed related to changes in food availability, particularly for rufous lemurs (Prediction 3b). Rufous lemurs used smaller patches that were more common and clumped when fruit was abundant (Prediction 2). Feeding subgroups were also smaller so that the group could spread out but remain cohesive (all group members were within visual distance of each other and the observer). When fruit was scarce, they used larger, rarer, more uniform patches although CDs remained greater than 1.0 (contrary to Prediction 2). One possible explanation for this trend is that these patches are large enough to accommodate all rufous lemur group members for longer periods of time, as evidenced by the larger subgroup sizes (this study) and longer feeding bouts (Overdorff, 1993a).

These larger, rarer patches, which also contain larger fruits, however, are not entirely sufficient because rufous lemurs migrated from the site when fruit was most scarce (April; Overdorff, 1993a,b). Therefore, patch size may be most critical to rufous lemurs during periods of food scarcity. However, if food is not adequately abundant within these larger patches so that all group members are satiated, they will migrate to

areas which presumably contain more or different kinds of food. In fact, rufous lemurs have been observed to leave one portion of RNP when fruit was scarce and travel up to 5 km away to areas containing introduced secondary species such as *Psidium* fruit (Merenlender, 1993; Overdorff, unpublished data).

Red-bellied lemurs also used different kinds of patches, but unlike rufous lemurs this variability was not as clearly correlated with food abundance (contrary to Prediction 3b). The only variable significantly correlated to food availability was patch size, which decreased with new leaf availability. This result does not seem biologically meaningful, however, given that they ate new leaves more often when new leaves were scarcest (Overdorff, 1993a). Red-bellied lemurs also used large patches when fruit was scarce, but these larger patches may not be as critical to them as they are to rufous lemurs due to their small group size. Because groups contain only two adult animals, a juvenile, and possibly an infant, they can feed longer per patch and visit fewer patches daily without migrating from the study area.

Two questions remain to be answered regarding the relationship between ecology and these two lemur species' social structure given the results of this study. First, why don't rufous lemurs adopt a fission-fusion social structure like spider monkeys and pygmy chimpanzees—if not consistently, at least seasonally, as an alternative to migration? Second, why aren't red-bellied lemur groups larger, given the presumed advantages attributed to slightly larger group size (Terborgh and Janson, 1986); or alternatively, what constrains red-bellied lemur group size?

As reported previously, rufous lemurs maintained cohesive groups during seasonal changes in food availability without fissioning by using patches in different ways. There are two possible reasons why rufous lemurs may wish to maintain group cohesion: predation avoidance and intergroup dominance. They may remain in cohesive groups to subvert predation because they are smaller in body size than most fission-fusion species (2 kg; Glander et al., 1992). This idea is supported by the recent findings of Good-

man et al. (1993; see Wright, 1995), who showed that predation pressure is more severe in eastern rain forests of Madagascar than previously thought. Rufous lemurs also appear to gain some advantage in interspecific and intraspecific encounters for food. Due to their larger group sizes, they can displace smaller groups from patches (Overdorff, unpublished data).

However, these explanations do not explain why red-bellied lemurs remain in small groups; they would be just as vulnerable to predation pressure as rufous lemurs since they are the same body size and are consistently supplanted from food sources by the larger groups (Overdorff, unpublished data). Further tests of the ecological model should include a comparison of large groups of red-bellied lemurs and small groups of rufous lemurs to determine if ecological differences are the result of niche separation or related to group size. Patch-use models would be more strongly supported if small groups of rufous lemurs behave similarly to small groups of red-bellied lemurs. Otherwise, the ecological patterns observed may be the result of species-specific differences in diet that would allow these two species to coexist but do not necessarily influence group size. However, researchers at the study site have never observed stable rufous lemur groups as small as red-bellied lemur groups or found red-bellied lemur groups comparable in size and composition to rufous lemur groups. Group sizes also appear to be relatively fixed in these species and related subspecies in other regions of Madagascar (Tattersall, 1982; Harcourt and Thornback, 1990; Merelender, 1993). Consequently, the explanation for the differences in rufous and red-bellied lemur social structure may not be entirely ecologically based, and other explanations must be investigated.

One alternative explanation is that infant development and reproductive effort may be correlated with and influence lemur social structure either independently or in conjunction with ecology. Although life-history traits are not entirely independent of ecological influences (Partridge and Harvey, 1988), they have been strongly correlated with variations in morphology and behavior in other primates and mammals (Harvey et al.,



1989a,b; Harvey and Purvis, 1991). For example, additional reproductive constraints may lead to the selection for alloparental care: an increased maternal/infant weight ratio (Leutenegger, 1980; Wright, 1984; Young et al., 1990), lactation length (Wright, 1990), milk content (Tilden, 1993), and infant growth and development rates prenatally and postnatally (Wright, 1984, 1990; Young et al., 1990).

It appears that infant developmental rates in these two lemur species are different as judged from the preliminary data presented in this study (Hypothesis II, Prediction 1). If female red-bellied lemurs are in fact producing more precocial or rapidly developing infants, more energy may be dedicated to their prenatal and postnatal care, as hypothesized by Young et al. (1990). Consequently, a monogamous social structure may be selected if additional care for infants by other group members is necessary to insure infant survival, as is the case in small-bodied New World primates (Fragaszy et al., 1982; Wright, 1984, 1986; Goldizen, 1987a,b). As reproductive rate decreases and reproductive effort increases, then a point will be reached where fathers or siblings can increase infant survival rates by assisting with infant care. Under these circumstances, however, it would be to the helper's advantage to assist only their own offspring or their close relatives' offspring (Hamilton, 1964).

Territoriality in combination with developmental patterns also may play a role in constraining red-bellied lemur group size. If a red-bellied lemur mother is supporting a precocial infant, access to resources could be critical. Territorial defense would insure her exclusive access to resources not used by other groups of red-bellied lemurs. If groups were larger, the range would increase proportionally and no longer be defensible (Mitani and Rodman, 1979). Therefore, this constraint, in addition to infant developmental patterns, may place an upper limit on the size of red-bellied lemur groups.

Gould (1991), however, has demonstrated that ring-tailed lemur (*Lemur catta*) infants develop at approximately the same rate as red-bellied lemur infants, yet ring-tailed lemurs are found in much larger groups. Al-

though ring-tailed lemur groups are larger, some assistance with offspring has been observed. Ring-tailed lemur females care for other offspring that are not their own, but little interaction occurs between males and infants (Sussman, 1977; Gould, 1991). In this case, larger group size may be related to terrestriality, and terrestrial primates tend to be more precocial (Chalmers, 1973). Obviously, red-bellied lemurs are not terrestrial, and more in-depth study of their developmental patterns must be conducted to discern why they are more precocial than other arboreal lemurid primates.

This study has shown that no single ecological factor, particularly patch size, is the strongest correlate to group size or social structure. Although patch size influences feeding rates, it does not influence intake in similar ways reported for other nonhuman primate species. Therefore, patch size may not be the best variable to use to estimate food abundance. Food item size, degree of quality, and predictability may be confounding variables that affect feeding rates and influence group size.

Both lemur species also demonstrated inconsistent patch-use patterns. Changes in how rufous lemurs used patches were linked more closely to fruit availability. Although red-bellied lemurs also used patches in different ways, they were not as affected by seasonal patterns. Differences in infant development may place an upper limit on group size in red-bellied lemur groups. With this constraint removed for rufous lemurs, they can form larger groups; however, the maximum size for rufous lemur groups may be constrained by the unpredictability and availability in food supply. Therefore, large or small groups can use various ecological strategies to maintain group cohesion throughout the year and cope with changes in food availability. In addition, life-history constraints such as differential patterns of growth and development of infants can predispose for certain social behaviors, such as the need for male care (albeit minimal care). These constraints may then limit group size in some species, while species living in larger groups may be constrained by the abundance, distribution, and availability of quality foods.

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